

First description of reproductive behavior of the Amazonian damselfly *Chalcopteryx rutilans* (Rambur) (Odonata, Polythoridae)

Daniela C. Resende¹ & Paulo De Marco Jr.²

¹Laboratório de Bioinformática e Evolução, Depto. de Biologia Geral, Universidade Federal de Viçosa, 36570-000 Viçosa-MG, Brazil. dcrese@ig.com.br

²Laboratório de Ecologia Teórica e Síntese, Instituto de Ciências Biológicas, Universidade Federal de Goiás, 74001-970 Goiânia-GO, Brazil. pdemarco@icb.ufg.br

ABSTRACT. First description of reproductive behavior of the Amazonian damselfly *Chalcopteryx rutilans* (Rambur) (Odonata, Polythoridae). Polythoridae comprise a widespread group of species in the New World tropics, but little is known about their behavior or life history. Here, we described the reproductive behavior of Amazonian *Chalcopteryx rutilans*, using mark-recapture techniques. Males were resident and territorial, though we found disputes (complex flight manoeuvres) to be rare. Trunks (rotting wood) were important to male persistence in sites, as these are the locations preferred by females for oviposition. The mating system of *C. rutilans* may be comparable to the *resource limitation* category, described by Conrad & Pritchard (1992), where males cannot control female access to oviposition sites. So, female choice becomes important and apparently, the observed displays (in which males flash the coppery coloration of their hind wings) may be related to attraction of females to territories, as in a lek system.

KEYWORDS. Amazonia; lek; residency; sexual selection; territory.

RESUMO. Primeira descrição do comportamento reprodutivo da libélula amazônica *Chalcopteryx rutilans* (Rambur) (Odonata, Polythoridae). A família Polythoridae compreende diversas espécies tropicais, das quais muito pouco se conhece sobre o comportamento ou história de vida. Neste trabalho, nós descrevemos o comportamento reprodutivo da espécie amazônica *Chalcopteryx rutilans*, utilizando técnica de marcação e recaptura. Os machos foram residentes e territorialistas, apesar das disputas (que envolvem manobras de voo complexas) serem raras. A ocorrência de troncos caídos sobre os igarapés foi importante para a persistência dos machos nos territórios, uma vez que as fêmeas utilizam estes locais para postura dos ovos. O sistema de acasalamento de *C. rutilans* parece similar ao “sistema com limitação de recurso”, descrito por Conrad & Pritchard (1992), onde os machos não são capazes de controlar o acesso das fêmeas aos recursos de oviposição. Nestes casos, as fêmeas podem escolher os machos e, aparentemente, as freqüentes exibições dos machos (mostrando a coloração interna cobreada de suas asas) podem estar relacionadas à atração de fêmeas aos territórios, semelhante ao sistema tipo lek.

PALAVRAS-CHAVE. Amazônia; lek; residência; seleção sexual; território.

The reproductive behavior of the order Odonata is frequently classified according to the existence and type of resource defense (Emlen & Oring 1977; Conrad & Pritchard 1992; Battin 1993). Resource defense in this group occurs when males defend oviposition sites and thereby gain access to receptive females that come to the area to lay their eggs. Resource defense system may be subdivided in: i) resource control, when males are able to control the access of females to all available oviposition resources, by the defense of territories and ii) resource limitation, in which co-occurrence of males and females is predictable in time and space, but males are not able to control the access of females to all oviposition resources (Conrad & Pritchard 1992).

One of the most studied Odonate groups is the damselfly family Calopterygidae. The mating behavior of some calopterygid species appears to fit the classic pattern of resource defense system (Conrad & Pritchard 1992). Females of *Calopteryx* Leach species (Calopterygidae, Odonata) usually oviposit into patches of macrophytes (Alcock 1987; Waage 1987; Meek & Herman 1991; Hooper & Siva-Jothy 1997) and males defend territories containing oviposition sites, display to and mate with incoming females, and guard females ovipositing in their territories (Pajunen 1966; Miyakawa 1982;

Meek & Herman 1991). The territorial disputes of calopterygid species comprise elaborate flights and/or displays where the outcomes of a contest is determined by the persistence of competitors dependent on their energy reserves (Conrad & Herman 1987; Waage 1988; Marden & Waage 1990). These wars of attrition communicate information about asymmetries among males, and body coloration and some types of displays can be involved in this information exchange. For example, it has been suggested that males of *Calopteryx maculata* (Palisot de Beauvois, 1807) with different body sizes present different body coloration and these characteristics are related to the ability of males to defend territories (Fitzstephens & Getty 2000). Larger males of another calopterygid, *Hetaerina americana* (Fabricius, 1798) presented larger wing spots, sustained longer territorial fights, were more successful at holding territories and obtained more copulations (Grether 1996a; Serrano-Meneses *et al.* 2007).

The territorial behavior or residency of odonate males can vary inter- or intra-specifically, depending on life history and individual characteristics such as age or body size (Meek & Herman 1991; Stoks 2000). In *C. maculata*, a resident-intruder asymmetry results in most contests being settled in a few seconds (Waage 1988) and, apparently, this asymmetry

exists because residents have highly variable energy reserves and because each contestant may not be able to quickly gauge the other's energetic status (Marden & Waage 1990). Displays can also assume an important role in conflict resolution between males, especially in reproductive systems lacking resource control (Hurd & Ydenberg 1996). Honest display information must represent an evolutionary stable strategy due to the mutual advantages resulting from minimizing harassment or injuries by territorial disputes (Jonhstone & Norris 1993).

Polythoridae is considered a sister-group of Calopterygidae (Rehn 2003) and although the behavior of Calopterygidae species has been intensively studied, little information has hitherto been published on the reproductive behavior or life history characteristics of Polythoridae species (Fraser & Herman 1993; Pritchard 1996). Males of *Cora Selys* (Polythoridae, Odonata) species may present a high degree of residence, returning repeatedly to the same perch in their territory (defended area), often over a number of days (Fraser & Herman 1993). These males defend territories centered around rooting wood in a creek bed, which is used by females as oviposition substrate (Fraser & Herman 1993). The aggressive behavior among males may comprise an escalated ascending spiral flight and the reproductive behavior apparently is not elaborated, without courtship or postcopulatory site display to females (Fraser & Herman 1993; Pritchard 1996).

Chalcopteryx rutilans Rambur, 1842 (Polythoridae, Odonata) is a common species in the Central Amazon region and occurs in continuous forest. This species has a small body size and males and females present a black coloration on the thorax, abdomen and hind wings (Santos & Machado 1960). The superior faces of the hind wings are very conspicuous with a "coppery" coloration and when an individual opens their wings, there is a brief, bright metallic flash, which is quite striking in the shadow of the forest canopy. This behavior seems to be quite frequent between males.

In this paper, we described the reproductive behavior of *C. rutilans*, trying to determine: i) if males are residents (if they defend the same territories for long time); ii) if there are territorial disputes among males; iii) if the exhibition of coppery coloration of wings may be some kind of signal between males (display); and iv) which characteristics are associated with territorial defense.

MATERIAL AND METHODS

We did this work along a small creek (igarapé) in Central Amazon, Brazil (020° 24'S; 590° 44'O), located in a Terra-Firme Forest, with predominant soil of Latossolo amarelo and altitude between 50 and 150 m above sea level (Lovejoy & Bierregaard 1990). The average temperature is 26.7° C and it was registered a minimum of 300 mm to rainfall in the dry months.

In November 2002, we visited 15 sites where we could find males of *C. rutilans* and studied the territorial behavior of this species. We captured 34 males with butterfly net and individually marked them with waterproof ink. We noted the site at which each male was captured and in the following

days we monitored all sites, registering each observed male. In the last day, we remained in only one site in an attempt to observe a copulation event. Behavioral observations were limited to about four hours daily, from 1000 to 1400 hrs.

The territorial behavior was observed by the focal method (Altmann 1974). During 20 minutes, we observed the behavioral sequence of an individual and the moment when behaviors changed was recorded, allowing us to construct a temporal budget. We classified the observed behavior into five categories: i) perching; ii) display: when a perched male exhibited the coppery coloration of wings, opening and closing them; iii) patrol: flying back and forth through an area; iv) interaction: interactions with conspecific males and v) flight: transitional flights.

We characterized the territorial sites (an area of around 2 m²) of *C. rutilans* males recording: i) the number of males and females present; ii) the presence of light, foliage, sand, trunks (rotting wood), and some types of vegetation inside the territorial sites (Bromeliaceae and Rapateaceae). We recorded the presence of trunks and vegetation because these substrates could be used by the female for oviposition, similar to other Polythoridae and Calopterygidae species (Alcock 1987; Fraser & Herman 1993). The relevance of these physical characteristics to territorial male choice was tested by the persistence of males in these territorial sites (if observed males persisted in the territorial sites during the 20 min observed). We assumed that, during the daily period of observation, the males can establish territories and rearrange themselves among territorial sites.

To evaluate the relationship between the territorial site characteristics and the persistence of males, we performed a Fisher Exact test. To verify if males defended territories and if displays are a kind of signal between males, we did regression analysis between time spent on territorial interactions and total number of males in the sites and between number of displays exhibited by males and total number of males in the sites. If the interactions among males or displays were aggressive behaviors, we presupposed that they would be more frequent on sites with many males, due to the high number of encounter among males.

RESULTS

Are males residents?

Males of *C. rutilans* were residents. Of 34 marked males, we recaptured 17 and only two of these males changed territorial site (Table I). The mean distance between territorial sites was 10.4 m (range 3.5 to 22 m) and the abundance of males in these sites was not uniform, varying between one and five individuals per site.

Do males dispute territories?

The observed interactions among males consisted in a series of flight manoeuvres, where a male in flight stopped in front of another male, trying to drive it back in a "face-off". This alternate chase caused circular movements around the defended area and the subsequent open-and-close wing

Table I. Summary of capture and recapture data of *C. rutilans* males during five days of study in the Central Amazon region, Brazil. We considered a male to have persisted in the territory when it was recaptured in the same site in which it was previously observed. *Data of 11/28/02 refers to only one territorial defense site.

Day	Number of captures	Number of recaptures (number of days since the capture)	Males persistent
11/24/02	13	-	-
11/25/02	7	4 (1)	4
11/26/02	12	2 (1); 3 (2)	3
11/27/02	3	2 (1); 6 (2); 5 (3)	13
11/28/02*	0	1 (2); 2 (3)	3

movements highlight the internal coppery color. These chases occurred just above the water surface or higher, to an approximate height of 3 m. We observed a total of 52 interactions (23 different individuals) and they were considerably variable, involving 2 to 4 males and ranging in duration from 2 to 780 seconds (mean = 21 s; SD = 126.9). We considered these interactions like a kind of ritualized territorial dispute.

Males of *C. rutilans* remained perched about 93% (N = 24) of total activity time and spent little time on all other behavioral categories. However, despite the low mean time spent on conspecific interactions (0.01 s), the standard deviation of this category was very high (0.244 s; Table II). This occurred because some males did not spend any time on conspecific interactions while other ones spent several minutes, so, this behavior can be seen frequently in the territorial sites.

Do males signal to other males?

Males spent more time on conspecific interactions when there were more males in the territorial site ($F_{1,21} = 9.42$; $p < 0.01$, $R^2 = 0.31$; Fig. 1), but, after these interactions none of the contestant males left the site. On the other hand, time spent on patrol was not affected by the number of males in the territorial site ($F_{1,21} = 1.89$; $p = 0.18$, $R^2 = 0.08$) and, similarly, the number of males within the territorial site did not affect the number of displays ($F_{1,21} = 0.17$; $p = 0.68$, $R^2 = 0.008$). So, despite the increase in time and energy spent in territorial interactions (disputes), males did not increase the number of displays exhibited at sites with more males.

What are the characteristics of a territorial site?

Presence of trunks (fallen trees) was important to the persistence of males in the territorial sites (Fisher Exact;

Table II. Temporal budget of reproductive behaviour to males of *C. rutilans* (N = 23) in the Central Amazon region, Brazil. Total time observed per individual: 20 minutes.

Behavioural category	Prop. Mean time	Standard deviation
Perch	0.928	0.248
Display	0.005	0.005
Patrol	0.013	0.051
Interaction	0.010	0.244
Flight	0.001	0.034

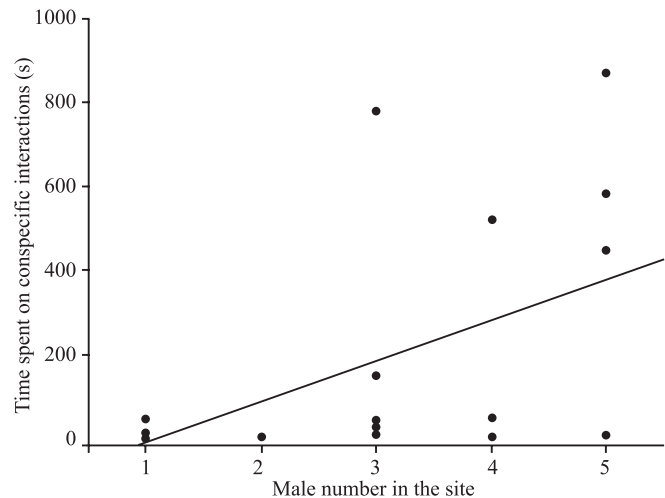


Fig. 1. Number of males in territorial site and time spent on aggressive interactions by males of *C. rutilans*, in Central Amazon region, Brazil.

$\chi^2=10.03$; $N=22$; $p=0.01$; Table III). Others characteristics analyzed, like presence of foliage (Fisher Exact; $\chi^2=0.46$; $N=22$; $p=0.48$), presence of sand (Fisher Exact; $\chi^2=0.36$; $N=22$; $p=1.00$), presence of light (Fisher Exact; $\chi^2=0.82$; $N=22$; $p=1.00$), presence of Bromeliaceae (Fisher Exact; $\chi^2=0.11$; $N=22$; $p=0.98$) and presence of Rapateaceae (Fisher Exact; $\chi^2=2.85$; $N=22$; $p=0.25$) did not affect male persistence in sites (Table III).

Reproductive behavior

Males of *C. rutilans* were observed perched on vegetation at the margins of the creek, below the forest canopy. Frequently, we observed more than one male in the same area (territorial site), up to a maximum of five males, but there was no correlation between number of males observed in a site and presence of the trunks ($t = 1.65$; $N = 22$; $p = 0.11$), foliage ($t = 0.44$; $N = 22$; $p = 0.66$), sand ($t = 1.27$; $N = 22$; $p = 0.22$); light ($t = 1.65$; $N = 22$; $p = 0.11$); Bromeliaceae ($t = 0.53$; $N = 22$; $p = 0.60$) or Rapateaceae ($t = 0.38$; $N = 22$; $p = 0.70$).

Females were not abundant in territorial sites. Only two occasions did we observe females in these sites and once we observed copula and oviposition. When we observed this behavior, the copula had already begun, so we could not verify if there was some kind of courtship before the copula. After 10 minutes, the male released the female but remained guarding her, chasing other males that approached. This female oviposited on a large fallen trunk over the stream and the ovipositor was thin and hard. During oviposition, this female folded the abdomen to insert eggs in the fissures of the bark of the tree. The other observed female seemed to oviposit alone.

DISCUSSION

The mating system of *C. rutilans* may be similar to the *resource limitation* described by Conrad & Pritchard (1992). In this resource-limitation system, males are not able to control female access to oviposition sites, because these sites

Table III. Physical characteristics in the territorial sites of males of *C. rutilans* and the importance of them to the probability of male persistence in the territory. The variable measured is the number of males persisting in the territorial sites during the 20 min observed (N=22) and in bracket is presented the percentage of persistence.

Site characteristics	Absence	Presence
Trunk	1 (25%)	16 (94.1%)
Foliage	2 (66.7%)	15 (83.3%)
Sand	10 (76.9%)	7 (87.5%)
Light	3 (100%)	14 (77.8%)
Bromeliaceae	14 (82%)	3 (75%)
Rapateaceae	5 (62.5%)	12 (92.3%)

may not be large enough to attract females or they could be too widely distributed - as fallen trees are in the Amazon forest - preventing male monopolization (Conrad & Pritchard 1992). So, females do not need to mate with a territorial male to reproduce successfully.

In this mating system, there should be strong selection on male characters, allowing them to obtain and hold territories (Conrad & Pritchard 1992). The high rate of recapture of *C. rutilans* males during five days and their territorial persistence show that this species has a high degree of residency. Once a territory has been defined as a defended area (Jacobs 1955), the increase of aggression with male encroachment at territorial sites suggests this species to have territorial behavior.

Previous residency is an important factor affecting conflict resolution, generally determining winners in territorial disputes (Gribbin & Thompson 1991; Mesterton-Gibbons *et al.* 1996). However, frequently, there were two or more *C. rutilans* males simultaneously at territorial sites, so previous residency must not be an asymmetrical characteristic defining territorial disputes, because all these males may consider themselves as residents. Furthermore, displays or wing coloration seem not to be providing information about male fighting ability, so this absence of previous information must increase the time spent on agonistic interactions.

There are several direct and indirect costs associated with escalated contests to calopterygid species: i) the speed, acceleration and complexity of manoeuvres far exceed what is normally observed during feeding, mating, or other activities and ii) prolonged contests may result into the loss of mating opportunities or in a third male becoming resident on the territory (Marden & Waage 1990). Consequently, the energetic and reproductive costs associated with prolonged escalations are high, decreasing the total time spent on a territory (Clausnitzer 1996) and potentially decreasing male reproductive success (Stoks 2000). So, we can think about a ritualized territorial dispute, like observed to *C. rutilans*, as an evolutionary strategy, mainly in a scenario where females are so rare.

When males are unable to control female access to oviposition sites, female choice may become important, allowing a strong sexual selection for morphological behavioral characteristics (Conrad & Pritchard 1992; Fincke 1997). Indeed, we observed a female ovipositing away from territorial males, so, *C. rutilans* females must be free

to choose a partner. Therefore, the wing coloration and the observed displays may be more related to the attraction of females to territorial sites, despite the fact that we could not test this due to the low number of observed females. Strong evidence for direct sexual selection on male wing coloration has already been demonstrated in the calopterygid species *H. americana* (Grether 1996b) and *Calopteryx haemorrhoidalis* Vander Linden, 1825 (Córdoba-Aguilar 2002).

Once females oviposit on trunks fallen over streams, the relationship between male territorial sites and trunks can explain the strong dependence of this species on forested areas (pers.obs.). The tree downfall is a frequent event in the Amazon Forest and this must supply the microhabitat used by this species. Despite this preference for territorial sites with fallen trunks, it is not clear why some sites presented a larger number of males than others.

An additional possibility may explain the reproductive behavior of *C. rutilans*. The concentration of males around some sites, the frequent signaling and the persistence of males in these sites despite long interactions with other males may represent a kind of lek mating system. If males do not control female access to oviposition sites, females may choose the quality of their mates and their oviposition sites separately (Conrad & Pritchard 1992). Ide and Kondoh (2000) predicted the environmental conditions that will favor lek system: i) male survivorship is sufficiently high during lekking; ii) female survivorship is sufficiently high while visiting a lek and, iii) lek efficiency is sufficiently high. Odonate male and female survivorship with this kind of lek system or with typical territorial behavior must not be so different, if males must remain at the stream edge and females must search for them, exposing them to predators. So, the main factor leading to the evolution of lekking behavior must be the efficiency of the method in securing mating. In an environment with so many streams and so many fallen trunks, male concentration could be a strategy to attract females to a specific site and the constant interactions and displays could be a strategy of male exhibitions to females. Recently, Córdoba-Aguilar *et al.* (2009) showed that males of *Hetaerina* species indeed display a lek mating system.

The post-copulatory mate guarding of *C. rutilans* seems to occur with males hovering over females, repelling opponents (non-contact guarding). The guarding behavior may be very important to reproductive success in calopterygid species, because males use their penis to remove all or almost all sperm stored by females, before transfer their own gametes (Waage 1979). Evolutionary theory generates the hypothesis that male damselflies should attempt to maximize the number of fertilized eggs, so mate guarding must be positively correlated with the chance of unguarded females mating with another male and also negatively correlated with the chance of missing additional mates during the guarding (Alcock 1982). The guarding behavior of *C. rutilans* males was expected because of female scarcity and because of the high male concentration at territorial sites. But, this guarding could be without contact, in fact, if female choose a specific partner in lekking.

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